THE ATTACHMENT OF OYSTER LARVÆ.

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Knowledge of the life history and ecology of the American oyster, *Ostrea virginica* Gmelin, is more extensive than in the case of any other species of lamellibranch. The researches of numerous investigators, notably of Brooks, J. Nelson, and Stafford, give us an almost unbroken history of this mollusc from the egg to the adult. As in most marine bivalves, the eggs of the oyster are shed into the water where fertilization occurs. Subsequent development is rapid, the larva forming a bivalve shell within two days or less. Then there follows a pelagic period of approximately two weeks during which the larva swims about with the aid of the velum, and increases considerably in size. At the close of the free-swimming period the larva settles upon some solid object and remains firmly attached at that point for the remainder of its life. Up to the time of attachment the history of most other marine lamellibranchs is similar to that of the oyster, but once the free-swimming period is ended we find a variety of behavior; the larvæ of *Pecten*, *Modiolus*, and *Mytilus* attach to seaweeds or to other objects, the larvæ of the Teredinidæ and of the Pholads bore within a solid substratum, while those of *Venus* and *Mya* burrow into the bottom.

Concerning the actual attachment of the oyster larva at the close of its pelagic life we have little information, the nature of the process having been deduced in the main from a study of the stages just preceding and just following fixation. Ryder, '82, Huxley, '83, Jackson, '90 and others, including the writer (Nelson, '21 A), believed that the secreting border of the mantle was used to cement the larva fast to the substratum. Stafford, '13, on the other hand, found in his youngest oyster "spat" that the left valve bore a layer about five times as thick as the shell itself, composed apparently of a different material. This thick layer

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covers more than one half of the outer surface of the left valve, extending from close to the anterior ventral edge almost to the umbo, but falling short posteriorly. From his study of the byssus gland in the base of the foot of the larval oyster, Stafford concluded that this organ must furnish the substance used to attach the larva, since the large amount of this material and its position far under the left valve preclude the use of the mantle for this purpose.

It has been my good fortune to observe the actual attachment of oyster larvæ under semi-natural conditions, and thus to be able to fill the gap in the information about this process. Large numbers of full grown oyster larvae were found at 8 P.M., July 23, in the water surrounding our laboratory houseboat on Barnegat Bay. A glass plate measuring 3 x 4 inches was lowered vertically into the water and removed half an hour later, and immediately suspended horizontally in a dish of sea water under the binocular.[1]

Six oyster larvae were moving about over the glass, holding on by means of the very active and highly adhesive ciliated foot. Some were on the upper, others on the lower side of the glass, thus permitting observation of the attachment process both from above and from below. With the velum withdrawn, and slowly

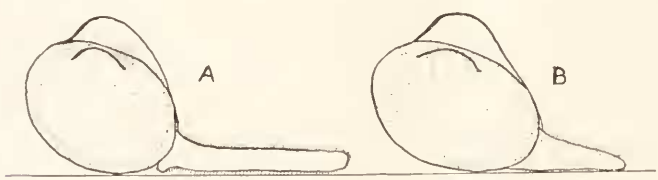

FIG. 1. Illustration of the method of creeping of the oyster larva over a glass surface. *A*, larva with foot fully extended; *B*, larva with foot contracted and body pulled forward. Larvæ shown from the right side.

rolling the shell from side to side, the larvæ extended the foot to a distance of about 0.25 mm., attached the distal end and then a contraction of the foot pulled the body forward. The "heel" of the foot next being attached, the body was swung part way around; the tip of the foot was again extended in the new direction and the process repeated (Fig. 1). When first observed at

[1] Jackson, '88, J. Nelson, '08, and Stafford, '10, used this method of obtaining oyster spat; but no one of these authors records having witnessed the actual attachment of the larva.

8.35 P.M. the larvæ were describing circles a little over 1 mm. in diameter. As they continued moving around the radius of the circles was gradually diminished, until at 8.46 the first larva came to rest With the foot extended to about one half its full length, its distal end flattened in contact with the glass, the larva swung the body until the foot occupied the median position, with the left valve against the glass and inclined to it at about 30 degrees (Fig. 2). In this position the ventral edge of the left valve almost touches the substratum. The ventral border of the mantle was extended until it came in contact with the glass where it remained for 2 minutes, and then was withdrawn. The foot, with its cilia beating very feebly, was then slowly drawn in, and 11 minutes after the larva ceased circling the foot had entirely disappeared between the valves, and fixation was accomplished. The method of attachment of the larvæ on the upper and on the lower side of the glass was the same; it illustrates, in the case of those larvæ attaching from below, the power of the foot in holding the left valve firmly against the substratum while fixation is being effected.

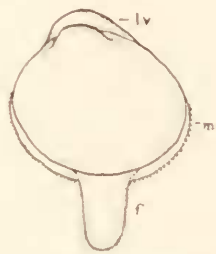

FIG. 2. The position taken by an oyster larva during fixation, shown from right side. *f*, foot; *l. v.*, umbo of left valve; *m*, mantle.

The great importance of the foot to the full-grown oyster larva was recognized by Stafford '10, who described its creeping movements. The manner in which the larva cements itself fast was deduced by him ('13, p. 65) solely from histological evidence. He concluded that the mantle could not furnish material in sufficient quantity nor rapidly enough to be of use as the organ of fixation. As he says: "The usefulness of the foot as an organ of locomotion, as a clinging organ, as an organ of fixation, had appealed to me for some time but I had no direct evidence to support the view that it was really the organ of final attachment."

Stafford found that a large part of the base of the foot of a full-grown oyster larva is occupied by the byssus gland which consists of three lobes communicating with a duct which opens to the outside at the heel of the foot. The cells of this gland are gorged with a transparent secretion which is not found in the much shrunken gland which characterizes the larva immediately after attachment. He believed that fixation was accomplished by the larva extending the foot until the heel came to a position near the upper anterior edge of the valve, and that the byssus gland then discharged its secretion, which, flowing between the left valve and the substratum, soon hardened and held the larva fast. Stafford believed that the mantle played no part in the fixation process.

My own observations show that Stafford was right in considering the foot as the organ of final attachment. It is not thrust forward, however, as he held, but is brought to the median position. The extrusion of the mantle for a short period evidently aids in the quick and economical distribution of the cementing fluid as it is poured out of the byssus gland at the ventral edge of the left valve. This secretion hardens in less than 10 minutes. In Fig. 3 are shown a number of newly attached larvæ

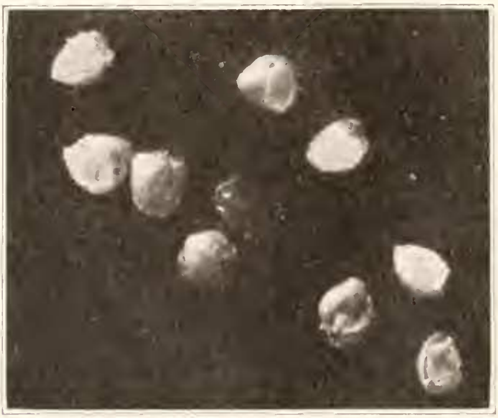

Fig. 3. Oyster larvæ removed just after attachment and photographed from the left side to show the area covered by the cementing substance from the byssus gland. Magnified about 40 diameters.

photographed from the left side to show the area covered by, and the distribution of, the cementing material.

The use of the foot in creeping over surfaces has been described in a number of larval bivalves, and it is the chief means by which the young molluscs obtain foothold in a favorable locality.

Kellogg, '99, showed the importance of the foot in aiding the larva of *Mya* to obtain attachment. Sigerfoos, '07, noted that larval shipworms possess a powerful foot by means of which they creep rapidly over surfaces and select spots favorable for fixation to the exclusion of those which are not suitable. Field, '09, states that the larvæ of *Mytilus* creep from unfavorable situations upon seaweeds to locations which are better adapted to them. Belding, '10, describes the foot of the larval *Pecten*, a most important organ, since it is used for swimming as well as in crawling. Belding, '12, showed that in the full-grown larva of *Venus* the foot likewise is used in swimming as well as for crawling, and for procuring attachment.

That the use of the foot enables oyster larvæ to exercise some selection in seeking a place of attachment is evident from the wide differences in the number of spat procured when various kinds of cultch are placed together in the water. I have recently shown (Nelson, '23,) that oyster larvæ will not attach to shells which are extensively pitted by the boring sponge, *Clione*, or which are badly corroded and which present surfaces that are microscopically rough.

For some hours before oyster larvæ set they may be observed moving about over various surfaces with the velum extended, its cilia beating actively; and with the foot protruded and bent at right angles, thus bringing the distal half in contact with the substratum. The foot remains quiescent in this position while the larva slowly "skates" along, as it were, propelled by the velum, but aided somewhat by the cilia on the foot. Then, swimming upwards, the larva progresses a short distance through the water and drops down to the substratum to continue as before. In this manner the larva may wander over an appreciable area before it eventually attaches (Nelson, '21 A).

In this connection it is well to correct the idea held by oyster growers and by some scientists also, that attachment of the oyster larva occurs when its shell becomes so heavy that the animal sinks to the bottom, unable longer to swim. For example, Stafford ('13, 34) says: "when presumably the larvæ become too heavy to swim with ease, settle towards the bottom, creep about, and select some clean solid surface upon which they fix themselves."

That such is not the case must be evident to anyone who has observed extensive oyster sets on the bottoms of boats, or upon the bottoms of floats kept at the very surface of the water (Nelson, '17,). The full-grown oyster larva, so far from being helpless, is capable of more powerful swimming than at any time during its pelagic life. During the course of the development and growth of the larva the increase in size of the velum is more than commensurate with the increase in the weight of the shell. Plankton samples taken during the calm of early morning show large numbers of full-grown oyster larvæ swimming at the surface. At times the larva may project the foot into the surface film and, withdrawing the velum, may hang suspended by the foot and slowly rock the shell from side to side, much as in the familiar habit of pond snails hanging from the surface film.

Full-grown oyster larvæ are found mostly at the bottom because they develop during the last two days of their pelagic life a strong positive stereotropism, and since fixed objects are most abundant on the bottom the larvæ mainly congregate there. The intensity of attachment which occurs at the very surface of the water when suitable cultch is available, precludes the idea that increased weight of the shell or even positive geotropism are factors exclusively governing the time of fixation.

The use of the foot by oyster larvæ in crawling over surfaces is similar to that reported by Crozier, '21, who found that the adult *Lima* oriented itself away from the light by attaching the tip of the foot to the substratum after bending the free portion away from the source of illumination. The creeping of oyster larvae is also strikingly similar to that observed in the fresh-water Sphæridæ, and especially in the young of *Corneocyclas* when first liberated from the brood pouches of the parent (Nelson, '21 B).

In sessile forms, such as the oyster, which remain fixed on the spot where the larvæ set, keen competition follows when large numbers settle at one time. During heavy sets 1,000 larvæ may attach to one oyster shell 8 cm. long, upon an area which will permit not more than 6 oysters to grow to breeding age. It is significant that at such times of abundant settlement, when the water over the oyster beds may show as high as 250 full-grown larvæ per liter, the frequency of attachment per unit area of available cultch does not exceed a certain maximum.

Fig. 4 shows in a circle 6 mm. in diameter a group of 40 oyster larvæ just attached to an experimental shell. Unfortunately I have never witnessed the behavior of two oyster larvæ coming into contact with each other while circling about over a surface, but an examination of shells taken at times of maximum settlement indicates that the movements of the larvæ prior to final fixation not only aid them in finding a spot suitable for attachment, but that this behavior also tends to keep the larvæ separated from one another. The proximity of a neighboring larva could presumably be recognized only through touch, hence it is conceivable that here and there individuals failing to come in contact while circling about might attach close to one another, as occurred in six instances in Fig. 4. Examination of the most

FIG. 4. Newly attached oyster larvæ on the surface of an oyster shell. Within this circle, 6 mm. in diameter, are 40 larvæ. Magnified about 15 diameters.

heavily set shells in our collection shows out of 500 newly attached larvæ only 57, or 11.4 per cent., which are within .5 mm. of another larva. This distance is taken since it represents the approximate radius of the circles described by the larvæ when first observed. Studies of the behavior of other bivalve larvæ during the attachment period should give interesting information as to the prevalence of this type of behavior.

Summary.

Full-grown larvæ of the oyster shortly before attachment move over an appreciable area of solid surface testing it out with the foot.

Actual attachment is preceded by circling movements, the larva finally coming to rest with the left valve held in contact with the substratum by the foot.

The suggestion of Stafford, 13, that the foot is the organ of attachment has been confirmed by direct observation. The use of the foot and of the mantle during fixation is here described.

The circling movements of the larva while crawling over a substratum not only aid it in obtaining a favorable foothold, but probably are also instrumental in producing a fairly even distribution of the spat.

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